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First record of pterosaurs (Diapsida, Archosauromorpha, Pterosauria) in the Middle Jurassic of Madagascar

Abstract – The finding of the first pterosaurian remains in Madagascar is here reported. Their occurrence is documented by four fossil teeth, recently collected in the Middle Jurassic (Bathonian) sediments extending along the eastern rim of the Mahajanga Basin (NW Madagascar). Two morphotypes, possibly belonging to the same taxon, are recognised, and are tentatively referred to the suborder Rhamphorhynchoidea. For their geological age, the Madagascan specimens represent the most ancient pterosaurs found so far in Africa.

Key words: Reptilia, Diapsida, Archosauromorpha, Pterosauria, Middle Jurassic, Mahajanga Basin, Madagascar, Gondwana.

Riassunto – Prima segnalazione di pterosauri (Diapsida, Archosauromorpha, Pterosauria) nel Giurassico medio del Madagascar.

È qui segnalato il ritrovamento dei primi resti di pterosauri in Madagascar. La loro presenza è documentata da quattro denti fossili, raccolti recentemente nei depositi del Giurassico medio (Batoniano) che si estendono lungo il margine orientale del Bacino di Mahajanga (Madagascar nord-occidentale). Sono stati riconosciuti due morfotipi che sarebbero riconducibili al medesimo taxon, appartenente probabilmente al sottordine dei ranforincoidei (Rhamphorhynchoidea). Per la loro età geologica gli esemplari malgasci rappresentano i più antichi pterosauri sinora segnalati in Africa.

Parole chiave: Rettili, diapsidi, arcosauromorfi, pterosauri, Giurassico medio, Bacino di Mahajanga, Madagascar, Gondwana.

Introduction

The Mahajanga Basin comprises a large region of north-western Madagascar, where deposition of continental, deltaic and partly marine sediments occurred without interruption since Permian times. In recent years, the Mahajanga Basin has become famous in the palaeontological literature for its Late Cretaceous

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(Maastrichtian) archosaur-rich outcrops (Maevarano Fm). On the contrary, the equally fossiliferous Late Triassic and Jurassic deposits (Isalo 'Group'), exposed over a several-hundred-kilometre-long arc along the eastern and southern margins of the basin, after the first reports by Lydekker (1895), Thevenin (1907) and Besairie (1936), with the exception of Lavocat (1955) have been almost ignored for a long time, and only in the last decade have received some attention (Flynn *et al.*, 1997, 1999; Buffetaut, 2003).

In particular, the Middle Jurassic deposits of the Mahajanga Basin contain a peculiar fossil vertebrate fauna, which is still poorly known. Teeth of crocodiles, plesiosaurs and possibly ichthyosaurs, as well as dinosaurian remains, were reported in the last century (Besairie, 1936, 1972; Lavocat, 1955); one jaw fragment referred to the most ancient tribosphenic mammal was found recently (Flynn *et al.*, 1999). In April 2003, a joined expedition of the Museo di Storia Naturale di Milano and the Museo Civico dei Fossili di Besano, promoted by an Italian private sponsor (BIOE s.r.l.), gave the authors the opportunity to prospect the Jurassic sediments of the Mahajanga Basin, and to collect the specimens here examined.

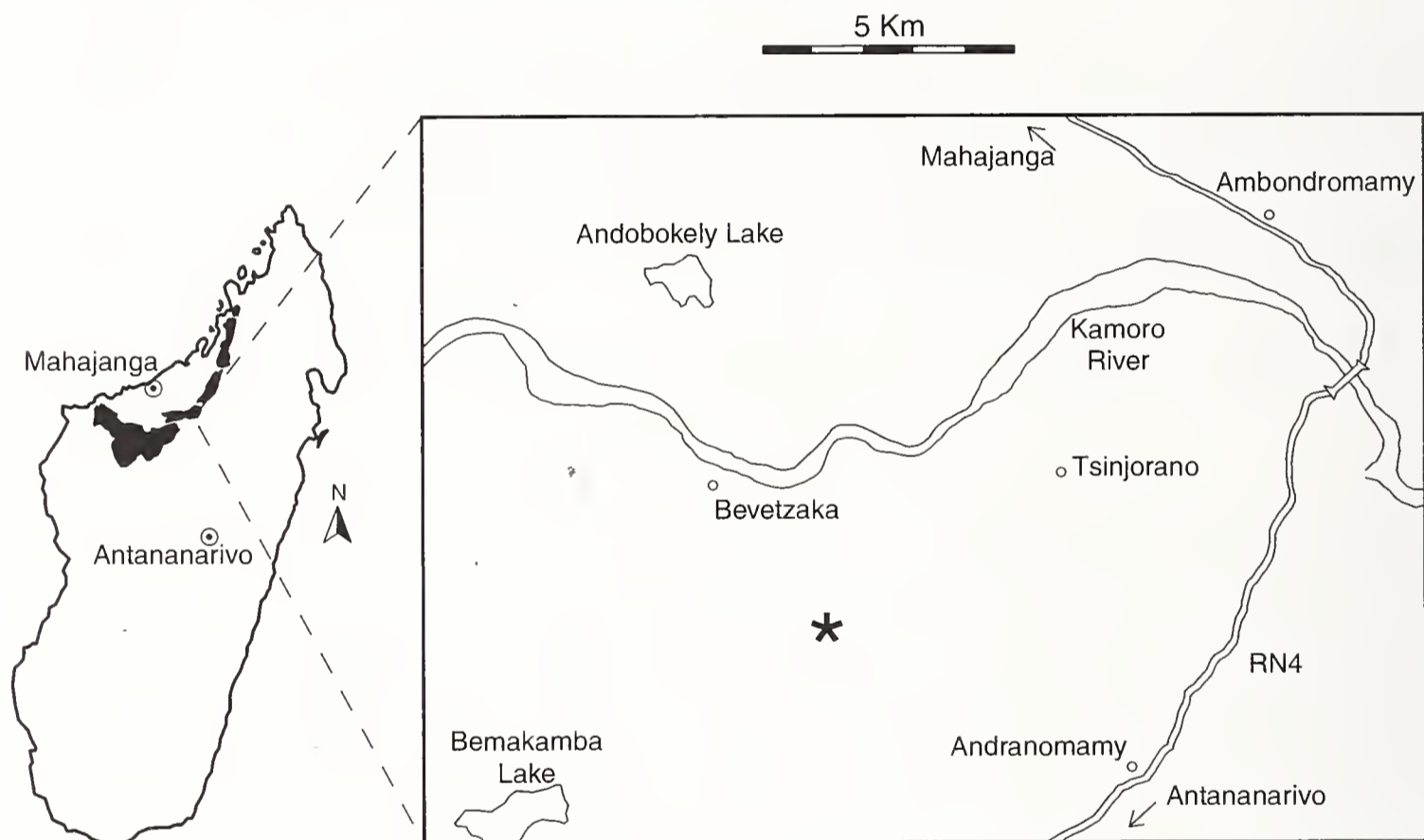


Fig. 1 – Map of the Triassic and Jurassic outcrops of the Mahajanga Basin (black areas on the left) and close-up of the localities recently prospected by the authors. The material here described comes from the site marked by the asterisk.

Fig. 1 – Mappa dei giacimenti triassici e giurassici del Bacino di Mahajanga (aree annerite nella cartina a sinistra) e particolare delle località recentemente prospettate dagli autori. Il materiale qui descritto proviene dal sito indicato dall'asterisco.

Geological setting

Between the villages of Ambondromamy and Ambalanjanakomby, about 170 km E-SE of Mahajanga, the national road to Tananarive (RN4) crosses a succession of *tanety* (local name for hills); actually they are true badlands created by weathering into the Jurassic sediments that constitute the eastern margin of the Mahajanga Basin (Fig. 1). These outcrops were correlated to the upper levels of the Isalo 'Group' (SW Madagascar) and named 'Isalo III-Facies Continental' by



Fig. 2 – The Middle Jurassic (Bathonian) Isalo IIIb subunit outcrops as a vast succession of *tanety* (hills) between the villages of Ambondromamy and Ambalanjanakomby.

Fig. 2 – La subunità stratigrafica chiamata Isalo IIIb, riferibile al Giurassico medio (Batoniano), affiora in una vasta successione di *tanety* (colline) tra i villaggi di Ambondromamy e Ambalanjanakomby.

Besairie (1936). Subsequently, the same author (Besairie, 1972) distinguished the top of the series as 'Isalo IIIb-Bathonien Facies Mixte Dinosauriens' because of its heterolithic nature, which was finally verified by Boast & Nairn (1982).

According to Besairie (1972) this subunit is about 190 m thick and consists of alternating, variegated sandstones and siltstones arranged in cross-bedding layers, calcareous paves and multicoloured claystone banks. Silicified wood is sometimes present, also according to our recent sampling. Besairie (1972) estimated a Bathonian age for the Isalo IIIb on the basis of its rich invertebrate fauna. In terms of absolute dating, these levels can be referred at $\sim 167 \pm 2$ Mya (Gradstein *et al.*, 1995). Besides the invertebrates, among which are the index fossils *Nucleolites amplus* and *Acrosalenia colcanapi* (Echinoidea), the Isalo IIIb fauna includes some vertebrates, so far represented only by fragmentary remains of Plesiosauria and Mesosuchia (?Steneosauridae), Theropoda, Sauropoda (*Bothriospondylus*) and Tribosphenida (*Ambondro mahabo*).

In October 2001, within an agreement between the Museo di Storia Naturale di Milano and the Ministère de l'Énergie et des Mines together with the Direction des Mines et de la Géologie de Madagascar, some inspection by one of the authors (G. Pasini) allowed to verify the presence and the extension of fossiliferous outcrops of the Isalo IIIb, and their potential for further research as well. Under that aim, four temporary concessions to prospection (Bureau du Cadastre Minier n. 3402-3405/Carte 41) were acquired in the area between Ambondromamy and Ambalanjanakomby. Following the first findings, a new prospection was arranged, that led to the recovery of the fossil specimens examined in the present paper.

The material was collected in April 2003, in the Isalo IIIb subunit composing the *tanety* located about 7 km W-NW of the village of Andranomamy, at an altitude of ~ 70 m (Fig. 2). The specimens were in relative association with one crocodylian osteoderm and several teeth, two possible mesosuchian teeth, and theropod and sauropod teeth and bones.

Materials and methods

The material here described is housed in the Collection of Fossil Vertebrates of the Museo di Storia Naturale di Milano (acronym MSNM V). The teeth, found isolated in loose sediments, are pictured in digital photographs (Nikon Coolpix 995, 3.34 Megapixels), which were taken on them as they were collected in the field. Therefore, no preparation techniques and possible related artifacts altered their surface. Also, the photographs are published without any electronic touching up. Measurements were taken with a digital caliper; cross-sections were obtained by casting the teeth with silicon RTV rubber and by subsequent cutting of their epoxy-resin replicas. The cross-section drawings were made under camera lucida.

Description

The teeth here described ranges from 16 to 20 mm in length and have slender shape, feeble curvature, pointed to domed end, and smooth surface. Their most important diagnostic character is a peculiar enamel pattern (the 'enamel cap'), that according to previous authors (Wellnhofer, 1985, 1991; Wellnhofer & Buffetaut,

1999) is restricted to the teeth of the Pterosauria. Because of intensive weathering the presence of a clear enamel cap, that is by itself very thin and is therefore easily erodible, is doubtful in one of the four specimens here examined (MSNM V5173); but its shape, curvature and compression ratio, as discussed below, allow to consider it very similar to MSNM V5170, which still preserves that typical enamel pattern. On the other hand, considering that the enamel capping can be found or not even within the tooth series of the same individual (Wellnhofer, 1985), we tentatively refer to the Pterosauria also the doubtful specimen.

Pterosauria KAUP 1834
Rhamphorhynchoidea PLIENINGER 1901
Morphotype I
(Figs. 3a-f, 4a-c, 5)

Material: Specimens MSNM V5170, V5171 and V5173, isolated teeth.

Age and stratigraphic horizon: Middle Jurassic (Bathonian), Mahajanga Basin, Isalo IIIb 'Facies Mixte Dinosauriens'.

Locality: 16°30'S, 49°68'E, hills W-NW of Andranomamy (Mahajanga Province), NW Madagascar.

Description: slender, elongate teeth with pointed end, gently recurved, with oval/elliptical cross-section (i.e., rounded lingually, but flattened labially) and with lateral compression constant all over the crown (Tab. I, compression index). At the base of these teeth, the posterior edge is slightly narrower than the anterior; at mid-length, the edges are more sharpened and develop an anterior and a posterior carina (Fig. 5), both covered by a thin enamel layer. In MSNM V5170, the tip of the crown is completely coated by an enamel cap, more extended towards the tooth base on the labial side. The enamel has a smooth and bright surface, while the dentine not covered by enamel is smooth and opaque. There are no traces of longitudinal ridges.

In labial view, the enamel border is oblique, with a feeble sigmoid course, and it is inclined (thus more extended) towards the anterior carina. The same enamel edge, although less evident than in V5170, is present in V5171, where weathering eroded and polished the original tooth coating.

On the lingual side, the enamel cap forms an inverted U-shaped margin at one-third length from the tip. The enamel edge is clearly evident only along the anterior carina of V5170, as the posterior carina is broken off together with a tip fragment. In any case, the lack of enamel on the medio-distal edge of the posterior carina suggests that its distribution is slightly asymmetrical; in other words, even in the unbroken tooth the posterior "arm" of the inverted U was shorter than the anterior one. A similar pattern, although less marked and even more asymmetrical, can be recognised in V5171. MSNM V5173 bears traces of a dark line, obliquely inclined towards the anterior carina, that might be remains of an enamel capping.

In lateral anterior view, the teeth of this morphotype appear feebly bowed, with gentle, constant curvature. The lower limit of the enamel cap forms a pointed end on the edge of the anterior carina, which reaches three quarters of tooth length (Figs. 3b, 3e, 4b, arrows). This pointed end is more evident in V5170, thanks also to its dark-brown colour, whereas in V5171 is visible as a lighter ivory spine.



Fig. 3 – Labial, lateral anterior and lingual views (left to right) of specimens MSNM V5170 (a-c) and V5171 (d-f). The arrows indicate the pointed distal end of the enamel coating. Scale bars are in mm.
 Fig. 3 – Viste labiali, laterali anteriori e linguali (da sinistra a destra) degli esemplari MSNM V5170 (a-c) e V5171 (d-f). Le frecce indicano la terminazione appuntita della copertura di smalto. Le scale metriche sono in mm.



Fig. 4 – Labial, lateral anterior and lingual views (left to right) of specimens MSNM V5173 (a-c) and V5172 (d-f). The arrows indicate the pointed distal end of the enamel coating. Scale bars are in mm.
 Fig. 4 – Viste labiali, laterali anteriori e linguali (da sinistra a destra) degli esemplari MSNM V5173 (a-c) e V5172 (d-f). Le frecce indicano la terminazione appuntita della copertura di smalto. Le scale metriche sono in mm.

Fragmented remains of the same structure, proving the former presence of an enamel capping, are preserved in V5173.

On the lateral posterior side, in all the specimens the tip and the upper edge of the posterior carina show a deeply oblique, almost vertical wearing surface.

Morphotype II (Figs. 4d-f, 5)

Material: Specimen MSNM V5172, isolated tooth.

Age and stratigraphic horizon: Middle Jurassic (Bathonian), Mahajanga Basin, Isalo IIIb 'Facies Mixte Dinosauriens'.

Locality: 16°30'S, 49°68'E, hills W-NW of Andranomamy (Mahajanga Province), NW Madagascar.

Description: elongate tooth, feebly curved as morphotype I but with larger base crown, that is developed antero-posteriorly, thus giving the tooth section a higher lateral compression (Tab. I). In cross-section, this tooth is then more elliptical than oval, nearly flattened (Fig. 5). MSNM V5172 has domed tip and little sharpened carinae, bordering the anterior and posterior edges except for the base of the crown. The enamel pattern is almost identical to that of the morphotype I, but the enamel coating and limits are less evident: due to weather consumption of the tooth surface, the dentine not covered by enamel became smooth and bright almost like the enamel, and the enamel itself was eroded and became more opaque.

In labial view, the trace of the border of the enamel cap can be seen as a faint oblique line at mid-length of the tooth. Like in MSNM V5170 and V5171, that line is inclined towards the anterior carina with an angle of 45-50 degrees and has a feebly sigmoid shape.

On the lingual side the enamel cap forms another oblique line, a bit arched and inclined anteriorly, rather than an inverted U.

In lateral anterior view the tooth V5172 appears constantly and gently curved. The enamel distal pointed end is still visible and a bit less eroded on the anterior carina, where it approaches the base of the crown (Fig. 4e, arrow).

On the lateral posterior side, also this specimen shows a wearing surface on the edge of the posterior carina, towards the tip.

Discussion

As pointed out in the descriptions above, the subdivision of our material in two morphotypes is not simply suggested by similarities of their outline and enamel pattern, but it is strengthened by their cross-section analysis (Fig. 5). From this point of view, MSNM V5170 and V5171 are almost identical, and MSNM V5173 is only slightly divergent (i.e., more rounded) because of deeper taphonomical smoothing.

These morphotypes are also supported by morphometric data (Tab. I). Specimen MSNM V5173, even though more slender, has the identical compression ratio of V5170 and almost the same of V5171. MSNM V5172 shows the highest compression and the lowest elongation ratio. Another character that emerges by the measurements is that these teeth have a remarkably perfect section continuity (base compression ratio and middle compression ratio are identical in every specimen).

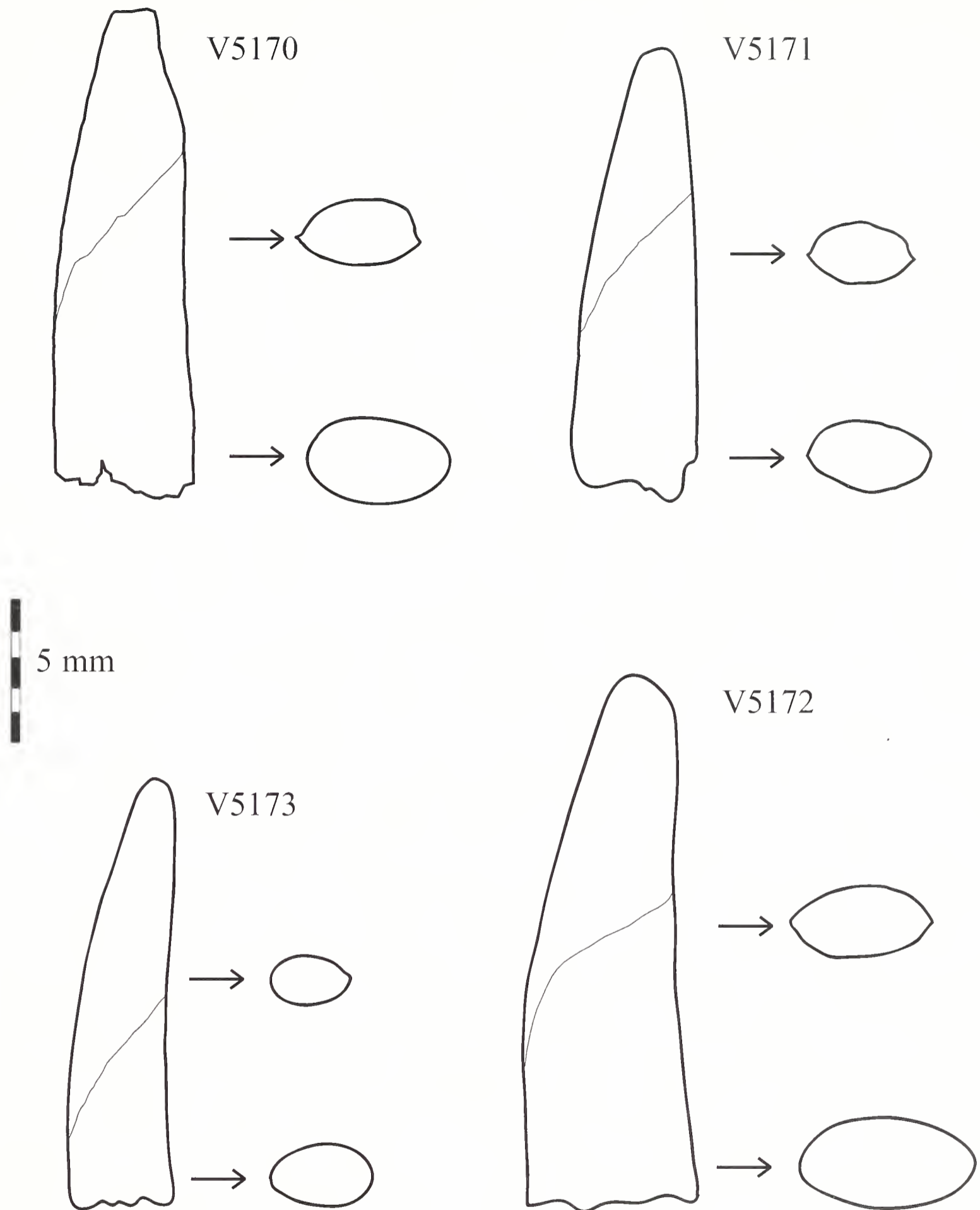


Fig. 5 – Labial views and cross-sections of the pterosaur teeth here described. For better comparison, MSNM V5172 and V5173 are drawn as mirror images of the actual specimens. The thin lines indicate the sigmoidal margin of the enamel cap. Scale bar = 5 mm.

Fig. 5 – Viste labiali e in sezione trasversa dei denti di pterosauri qui descritti. Per agevolare il confronto, MSNM V5172 e V5173 sono stati disegnati come immagini speculari degli esemplari reali. Le linee sottili indicano il margine sigmoidale del cappuccio di smalto. Scala metrica = 5 mm.

Tab. I – Basic measurements of the teeth described above.

Tab. I – Misure principali dei denti sopra descritti.

| MSNM | V5170 | V5171 | V5172 | V5173 |
|---|-------|-------|-------|-------|
| Tooth length | 17.50 | 16.49 | 19.80 | 15.77 |
| Base maximum (rostro-caudal) diameter | 5.17 | 4.40 | 6.42 | 3.77 |
| Base minimum (labio-lingual) diameter | 2.97 | 2.45 | 3.38 | 2.18 |
| Middle maximum (rostro-caudal) diameter | 4.45 | 3.52 | 5.38 | 3.04 |
| Middle minimum (labio-lingual) diameter | 2.53 | 1.96 | 2.80 | 1.75 |
| Base compression ratio (min:max diameter) | 0.57 | 0.55 | 0.52 | 0.58 |
| Middle compression ratio (min:max diameter) | 0.57 | 0.55 | 0.52 | 0.57 |
| Elongation ratio (base max diameter:tooth length) | 0.29 | 0.27 | 0.32 | 0.24 |

As the teeth of the pterosaurs vary considerably in size and shape according to their position in the jaws (Wellnhofer, 1985, 1991, 1996), it is possible that the two morphotypes (feebly carinate teeth, which differ substantially only in the degree of lateral compression) belong to a single species. Also, it is not allowed to know whether the individual teeth came from the upper or the lower jaw.

According to the variation observed within the tooth series of the most complete pterosaurian skulls (Wellnhofer, 1970, 1975a, 1975b), we hypothesise that the morphotype I would be equipped in the middle portion of the jaws, and that the morphotype II would be placed more backwards, with a slicing rather than grasping function.

The Madagascan teeth cannot be assigned to a specific taxon beyond the systematic rank of the Rhamphorhynchoidea. Our specimens could be hardly referred to the Pterodactyloidea because of some important differences, such as the absence of longitudinal striations at the base of the crowns, and because of their stratigraphic position: according to Wellnhofer (2003, pers. com.), the Pterodactyloidea have their first occurrence in the Late Jurassic (Kimmeridgian).

In fact, for comparison purpose, we examined some teeth from the Cretaceous (Cenomanian) red beds of Kem-Kem, Morocco, that are housed in the Museo di Storia Naturale di Milano with the collection n. MSNM V3688, V3680 and V3681. The geological age of this material is definitely different, but its better preservation, due to much lesser weathering, allows to better point out some anatomical differences and similarities with the Madagascan material.

Given their geological age and their resemblance with previously studied teeth (Wellnhofer & Buffetaut, 1999), there is no doubt that the Moroccan specimens belong to pterodactyloid pterosaurs. In both the published and directly observed teeth, the base crowns are ornamented by longitudinal striations, that are more evident on the lingual sides, and that are completely absent in the Madagascan specimens.

A second difference is in the enamel pattern, that in our teeth is not symmetrical (antero-posteriorly) as in the Moroccan specimens. On the labial side of the Madagascan teeth, the enamel edge is always strongly oblique, and on the lingual side the posterior arm of the inverted U is very short (morphotype I) or absent (morphotype II). In the Moroccan material, from our observations both in the published (Wellnhofer & Buffetaut, 1999) and directly examined teeth (MSNM collection), in lingual view the enamel cap has a more constant pattern, well represented by a complete inverted U. Whether the shape and the extension of the cap

might be related only to the tooth position (see below) or might have also a systematic value, it remains a pure speculation.

In terms of functional anatomy, the different labio-lingual distribution of the enamel on some pterosaur teeth have received so far few attention. Such analysis is beyond the aim of the present paper; however it is clear that, similarly to other living and extinct tetrapods, also in the flying reptiles the enamel cap had a strengthening function for their pointed and slender teeth. As in pterosaurs the grasping function was primarily left to the front teeth, this may be a possible explanation for the lack of enamel in the posterior ones (Wellnhofer, 1985, Fig. 7d).

We noted some similarity with the Moroccan pterosaur teeth in the general shape. Our morphotype I matches well the morphotype I of Wellnhofer & Buffetaut (1999), which in the Milano collection may be represented by a specimen from Kem-Kem labelled MSNM V3688; it lacks the enamel cap but it has the same elongation and compression ratios (0.27, 0.55), and curvature, and it preserves carinae as well. Morphotype II has some analogy with the morphotype III of Wellnhofer & Buffetaut (1999) and with MSNM V3680, a Moroccan tooth that presents the same high compression ratio (0.51) and a similar enamel pattern.

Middle Jurassic Pterosaurs

It is possible that direct comparison of our material with Middle-Late Jurassic rhamphorhynchoids, that are likely more strictly related to the Madagascan pterosaurs, would allow closer determination. As a matter of fact we remark that, with the possible exception of *Herbstosaurus pigmaeus* (see below), at present there is no notice of pterodactyloid pterosaurs in the Middle Jurassic of any country. As listed by Wellnhofer (1991) and recently updated by Unwin (1996), the record of the Middle Jurassic pterosaurs is scrappy and limited to less than a dozen of taxa, all referred to the Rhamphorhynchoidea except for one genus of dsungaripteroid affinities, which might represent the earliest pterodactyloid. Many of them were studied in the nineteenth century (Andrews, 1911; Bakhurina & Unwin, 1995; Casamiquela, 1975; Fastovsky *et al.*, 1987; He *et al.*, 1983; Huxley, 1859; Lydekker, 1890; Meyer, 1832; Seeley, 1880).

Pterosauria KAUP 1834

Subordo et fam. indet.

Pteraichnus stokesi LOCKLEY, LOGUE, MORATALLA, HUNT, SCHULTZ & ROBINSON 1995

Callovian, Sundance Fm., Alcova Lake (Wyoming), USA.

Rhamphorhynchoidea PLIENINGER 1901

?Anurognathidae KUHN 1937

Gen. et sp. indet.

Aalenian-Bajocian, Bakhar Fm., Bakhar (Bayan-Khongor), Mongolia.

?Campylognathoididae UNWIN 1992

Gen. et sp. indet.

Aalenian-Bajocian, La Boca Fm., Huizachal Canyon (Tamaulipas), Mexico.

Rhamphorhynchidae SEELEY 1870

Angustinaripterus longicephalus HE, YAN & SU 1983

Bathonian, Lower Shaximiao Fm., Dashanpu near Zhigong (Sichuan), China.

Rhamphocephalus bucklandi MEYER 1832

Bathonian, Stonesfield Slate, Stonesfield (Oxfordshire), England.

Rhamphocephalus depressirostris HUXLEY 1859

Bathonian, Stonesfield Slate, Sarsden near Chipping Norton (Oxfordshire), England.

'Rhamphorhynchus' jessoni LYDEKKER 1890

Callovian, Middle Oxford Clay, St. Ives Brickyard (Cambridgeshire), England.

Gen. et sp. indet.

Callovian, Lower Oxford Clay, Peterborough, England.

Pterodactyloidea PLIENINGER 1901

Fam. indet.

Herbstosaurus pigmaeus CASAMIQUELA 1975

Callovian, Lotena Fm., Arrojo Picùn Leufù (Neuquén), Argentina.

At first sight, the general shape of our morphotypes I and II seems comparable to that of mid-posterior teeth of the rhamphorhynchids *Angustinaripterus* and *Rhamphocephalus*. Anurognathids can be easily excluded because of their very small, short, peg-like teeth.

Taking into account the peculiar palaeogeographic position of Madagascar within the Gondwanan landmass during the Mesozoic Era, it is worth mentioning the Early Jurassic campylognathoidid *Campylognathoides indicus* (Jain *et al.*, 1974). This Indian pterosaur, recovered from the Kota Formation in the Chanda district (Deccan), consists of a fragmentary specimen of a skull, which still preserves some teeth. Together with the better preserved co-generic forms from the Lias of Holzmaden, Germany (Plieninger, 1895), *Campylognathoides indicus* shows rather labio-lingually flattened teeth, without longitudinal striations, that are consistent with our morphotypes I and II. If the Huizachal pterosaur belongs in the Campylognathoididae (Unwin, 1996) then at least a second family, besides the Rhamphorhynchidae, may be considered as potentially present in the Bathonian of Madagascar.

Previous records of pterosaurs in Africa

Until less more than a decade ago, proof that pterosaurs also lived on the African continent rested upon very scarce examples (Wellnhofer, 1991). With the exception of a single Late Jurassic locality in Tanzania (Galton, 1980; Reck, 1931), pterosaur fossil remains were limited only to a couple of bones: a wing metacarpal from the Early Cretaceous of Zaire (Swinton, 1948) and a cervical vertebra from the Late Cretaceous of Senegal (Monteillet *et al.*, 1982). In recent years, intensive fossil collecting in Morocco extended the occurrence (Kellner & Mader, 1996) and diversity

(Mader & Kellner, 1997; Unwin & Heinrich, 1999; Wellnhofer & Buffetaut, 1999) of pterosaurs in Africa. The known taxa, all represented by fragmentary remains, are listed in the summary below (the *nomina dubia* are in quotes).

Late Jurassic

Rhamphorhynchoidea PLIENINGER 1901

Fam. indet.

'*Rhamphorhynchus tendagurensis*' RECK 1931

Kimmeridgian-Tithonian, Obere Saurier-Mergel, Tendaguru, Tanzania.

Pterodactyloidea PLIENINGER 1901

Dsungaripteridae YOUNG 1964

'*Dsungaripterus brancai*' GALTON 1980

Kimmeridgian-Tithonian, Obere Saurier-Mergel, Tendaguru, Tanzania.

'*Pterodactylus brancai*' RECK 1931

Kimmeridgian-Tithonian, Obere Saurier-Mergel, Tendaguru, Tanzania.

Tendaguripterus recki UNWIN & HEINRICH 1999

Kimmeridgian-Tithonian, Obere Saurier-Mergel, Tendaguru, Tanzania.

Fam. indet.

'*Pterodactylus arningi*' RECK 1931

Kimmeridgian-Tithonian, Obere Saurier-Mergel, Tendaguru, Tanzania.

'*Pterodactylus maximus*' RECK 1931

Kimmeridgian-Tithonian, Obere Saurier-Mergel, Tendaguru, Tanzania.

Early Cretaceous

Pterodactyloidea PLIENINGER 1901

Anhangueridae CAMPOS & KELLNER 1985

Siroccopteryx moroccensis MADER & KELLNER 1985

Early Cenomanian, Kem-Kem Beds, Morocco.

?Azhdarchidae PADIAN, 1986

Gen. et sp. indet.

Early Cenomanian, Kem-Kem Beds, Morocco.

Gen. et sp. indet.

Campanian-Maastrichtian, Paki, Senegal.

?Ornithocheiridae SEELEY 1870

Ornithocheirus sp.

Cenomanian-Turonian, Zaire.

Gen. et sp. indet.

Early Cenomanian, Kem-Kem Beds, Morocco.

?Pteranodontidae MARSH 1876

Gen. et sp. indet.

Early Cenomanian, Kem-Kem Beds, Morocco.

?Tapejaridae KELLNER 1989

Gen. et sp. indet.

Early Cenomanian, Kem-Kem Beds, Morocco.

The pterosaurian remains in Africa show a remarkable biodiversity, but quantitatively they still represent a very little portion of the Mesozoic vertebrate fauna. If compared to the ample documentation from South America, their sparse fossil record is surprisingly poor, particularly in the Early Cretaceous, a time when the two continents were still united. More field research in Africa is therefore expected to increase largely the number of findings, and given the very scarce remains of Middle Jurassic pterosaurs, the Mahajanga Basin represents a unique, promising area.

Conclusions

The present study demonstrates that toothed pterosaurs lived in Madagascar at least since Middle Jurassic times. Considering the stratigraphic position of the material, at present we prefer to ascribe our specimens to undetermined Middle Jurassic rhamphorhynchoids, and to simply speculate some affinity with coeval forms, such as the rhamphorhynchids *Rhamphocephalus* and *Angustinaripterus*. These are the only two genera, from that time, of which the teeth are known and seem to show some resemblance in shape and size with the specimens here described. Thus the moderate dimensions of the latter suggest their attribution to medium-sized pterosaurs. In any case, the geological age of the Madagascan fossils is particularly important, as they represent the most ancient pterosaurs from the African continent.

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